

OCCUPANCY AND ABUNDANCE OF DHOLE (*CUON ALPINUS*) IN PENCH LANDSCAPE OF CENTRAL INDIA

ANIRUDDHA MAJUMDER^{1,2}, QAMAR QURESHI^{1,3}, KALYANASUNDARAM SANKAR^{1,4},
SANTANU BASU^{1,5} AND YADAVENDRADEV V. JHALA^{1,6}

¹Wildlife Institute of India, P.O. Box # 18, Chandrabani, Dehradun 248 001, Uttarakhand, India.

²Email: aniruddha@wii.gov.in

³Email: qnq@wii.gov.in

⁴Email: sankark@wii.gov.in

⁵Email: santanubasu2k6@gmail.com

⁶Email: jhalay@wii.gov.in

Occupancy and abundance of dhole was studied in the Pench landscape of Central India between 2006 and 2010. Royle-Nichols heterogeneity model was used for abundance estimation of dhole. The 4,300 sq. km area of the Landscape was divided into 10 km x 10 km grids (n=43), considering each grid size is larger than the home range size of an individual dhole.

Different forest routes on each grid were surveyed to collect indirect evidences (spoor, fresh scats, etc.) of dhole, and each search covered 5 km distance (total effort 3,720 km) during 2006. The average dhole pack size was 13.9 ± 1.4 (Standard Error or SE). The estimated individual density of dhole in the Pench landscape was 3.3 ± 1.2 (SE)/100 sq. km. Naïve or site occupancy of dhole was estimated using indirect evidences from the Intensive Study Area or ISA (410 sq. km), i.e., in Pench National Park (PNP) and Pench Wildlife Sanctuary (PWS) of Pench Tiger Reserve, Madhya Pradesh, between February and June 2006, 2007, 2009 and 2010. Sampling occasions (n=3) were same for all four years and total effort varied between 725 km and 750 km. The estimated naïve or site occupancy of dhole in ISA was 0.81 ± 0.07 (SE) in 2006 followed by 0.96 ± 0.15 in 2007, 0.52 ± 0.08 in 2009 and 0.82 ± 0.14 in 2010.

Our study revealed that occupancy of dhole is high inside the Pench Protected Area (i.e., PNP and PWS), but low and patchy outside. As dhole population is observed fragmented, linkage between the different Protected Areas in this landscape is crucial for its long term survival.

Key words: *Cuon alpinus*, Pench landscape, abundance, occupancy, central India

INTRODUCTION

With the decline of most large carnivore population worldwide (Nowell and Jackson 1996) there is always an urgent need for practical and accurate methods of estimating population numbers and monitoring trends (Caughley and Sinclair 1994). Estimates of abundance are extremely valuable for species conservation, yet determining the abundance of elusive and wide-ranging carnivores is difficult, but possible, especially for those that can be identified by individual marking, like Tiger *Panthera tigris* (Karanth 1995; Sharma *et al.* 2010; Jhala *et al.* 2011), Leopard *Panthera pardus* (Mondol 2006; Edgaonkar 2008; Harihar *et al.* 2009; Ramesh 2010), Jaguar *Panthera onca* (Soisalo and Cavalcanti 2006) and Cheetah *Acinonyx jubatus* (Marnewick *et al.* 2008). Kelly *et al.* (2008) assessed reliability of Puma *Puma concolor* identification by photo-trapping using double-blind observer identifications. They also reported that obvious and subtle markings (scar, cut marks and wounds) of the species can be compared from camera trap photographs if the photo quality is good. Carbone *et al.* (2001) used photographic rates to estimate densities of cryptic

mammals, which require large sample size. Rowcliffe *et al.* (2008) also estimated animal density, without the need for individual recognition, from camera trapping rates by modelling the underlying detection process. Radio telemetry study was also used to estimate population of some large-bodied canids like Dhole *Cuon alpinus* (Acharya *et al.* 2007), Wolf *Canis lupus* (Mech 1977), Coyote *Canis latrans* (Andelt 1985). Radio-telemetry is constrained by the small number of animals that can be tagged simultaneously, the uncertainties about how many individuals are tagged, and the high costs and efforts involved (Karanth 1995). Kohn *et al.* (1999) estimated coyote population by genotyping faeces. Though this method may be more reliable for population estimation, because of its non-invasiveness (Miththapala 1996), the major drawback is high cost and need of skilled technicians and advanced laboratories (Kohn *et al.* 1999).

The only information on dhole abundance comes from a few protected areas in southern and central India (Johnsingh 1983, Karanth 1993, Venkatraman *et al.* 1995, Acharya *et al.* 2007). These estimates have not been obtained through systematic sample based survey methods, but on estimates of

number of packs within the protected areas (derived using known home range areas and knowledge of mean pack sizes) (Durbin *et al.* 2004). Ramesh (2010) estimated population of Dhole using vehicle transect method.

As dholes are the least studied social carnivores in the Asian jungles (Acharya *et al.* 2007), the present study was carried out in the Pench landscape of central India, between June 2006 and June 2010, to estimate occupancy and abundance of dholes using reliable scientific methods.

MATERIAL AND METHODS

Study area

The study area, Pench landscape (4,300 sq. km) is one of the important conservation units for carnivores and its prey in the central Indian landscape (Jhala *et al.* 2010) (Fig. 1). According to Champion and Seth (1968) classification, the study area falls under tropical dry deciduous forest and tropical moist deciduous forest. It includes Pench Tiger Reserve, South Seoni Forest Division, South Balaghat Forest Division, East Chindwara Forest Division and South Chindwara Forest Division. This Landscape lies in the southern lower reaches of Satpura Hill ranges. According to the biogeographic classification of Rodgers and Panwar (1988), it lies in the Zone - 6E Deccan Peninsula Central Highland. The terrain is gently undulating and criss-crossed by small streams and nullahs, most of these are seasonal. The study area experiences markedly seasonal climate with a distinct summer (March-June), monsoon (July-September) and winter (October-February) and receives a mean annual rainfall of c. 1,400 mm. The temperature ranged from 2 °C in winter to 49.5 °C in summer. Pench Tiger Reserve (PTR), which includes Pench National Park (PNP) and Pench Wildlife Sanctuary (PWS), along with Kanha Tiger Reserve constitutes one of the 11 level-I Tiger Conservation Units (TCU) in India classified by Wickramanayake *et al.* (1998). The PNP and PWS were considered as the intensive study area (410 sq. km) for the present study. Apart from dhole the other carnivore species found in this landscape are tiger, leopard, wolf, jackal (*Canis aureus*), Striped Hyena (*Hyaena hyaena*), Indian fox (*Vulpes bengalensis*) and Jungle cat (*Felis chaus*). The wild ungulates found here are Chital (*Axis axis*), Sambar (*Rusa unicolor*), Nilgai (*Boselaphus tragocamelus*), Gaur (*Bos frontalis*), Barking Deer (*Muntiacus muntjak*), Chousingha (*Tetracerus quadricornis*), Wild Pig (*Sus scrofa*), Blackbuck (*Antelope cervicapra*) and Chinkara (*Gazella bennettii*) (Sankar *et al.* 2001; Dungariyal 2008; Jhala *et al.* 2010). The Common Langur (*Semnopithecus entellus*) and Rhesus Macaque (*Macaca mulatta*) represent the primate fauna of the area. The Indian Crested Porcupine *Hystrix*

indica, Black-naped Hare (*Lepus nigricollis*), Indian Flying Fox (*Pteropus giganteus*), Red Giant Flying Squirrel (*Petaurista petaurista*), Three-striped Squirrel (*Funambulus palmarum*) and Indian Pangolin (*Manis crassicaudata*) also occur in this area. There are over 51,648 inhabitants in 107 villages and 60,000 livestock present around the notified buffer zone of PTR (Dungariyal 2008). The mean human population density is 112 ± 9 (Standard Error or SE) / sq. km and Gond tribes are the main inhabitants of this landscape (Qureshi *et al.* 2006; Jhala *et al.* 2010).

Methods

We used Royle-Nichols (Royle and Nichols 2003) heterogeneity model for abundance estimation of dhole. The key assumptions of the Royle-Nichols model are (1) the number of animals at a particular site follow a Poisson probability distribution for which lambda indicates the mean abundance across all sites, and (2) the probability of detecting animals at each site is related to the species specific capture probability 'r' and the site abundance (Ni).

Royle-Nichols heterogeneity model was used for larger data set (4,300 sq. km) for 2006 from 'Monitoring tiger, co-predator, prey and their habitat' - research project (Jhala *et al.* 2008). The parameter derived from larger study area was used to infer abundance of dhole in the intensive study area (410 sq. km). This larger study area was further sub-divided into 10 km x 10 km grids (n=43) (Fig. 1) and our assumption was that the grid size should be more than the home range size of a dhole pack. The average home range of dhole pack was 63 sq. km as reported by Acharya *et al.* (2007) in the same study area. Forest beats were considered as the lowest sampling unit for sign survey (Jhala *et al.* 2008) and three separate routes of each forest beat were walked early in the morning to record the signs and tracks of dhole. Each search covered 5 km having the best potential for dhole presence. Data collection was done covering 3,720 km. The site (naïve) occupancy (Mackenzie *et al.* 2002) of dhole population was estimated from beat wise (n=44) sign survey in the ISA in 2006, 2007, 2009 and 2010. Sampling occasions (n=3) were same for all the four years and total effort varied between 725 km and 750 km. The program PRESENCE ver. 3 was used for occupancy and abundance estimation (Jhala *et al.* 2010). T-test (Zar 1984) was used to evaluate temporal changes in occupancy.

RESULTS

The estimated occupancy of dhole in the overall landscape was 0.21 ± 0.06 (SE). Detection probability was 0.74 ± 0.09 (SE) and average dhole pack size was 13.9 ± 1.4

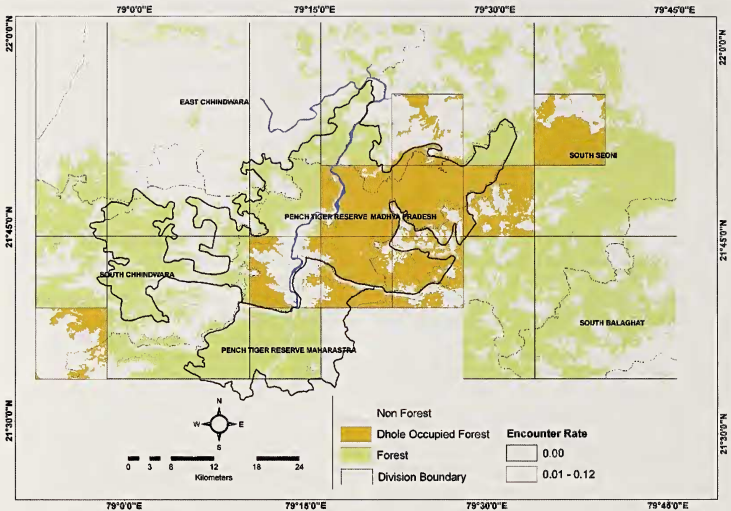


Fig. 1: Map showing grid wise ($n=43$) occupancy and encounter rate (signs/100 sq. km) of Dhole in Pench landscape (4,300 sq. km)

(SE). The estimated average abundance of dhole in the landscape was 0.24 ± 0.08 (SE)/100 sq. km. The estimated individual density of dhole in the overall landscape (multiplying average pack size of dhole with average abundance) was 3.3 ± 1.2 (SE)/100 sq. km for 2006 (Table 1).

The estimated naïve or site occupancy of dhole in the ISA, i.e., Pench National Park and Sanctuary for 2006 was 0.81 ± 0.07 (SE) followed by 0.96 ± 0.15 (SE) in 2007,

0.52 ± 0.08 in 2009 and 0.82 ± 0.14 in 2010, whereas detection probabilities were 0.65 ± 0.05 (SE) in 2006, 0.35 ± 0.06 (SE) in 2007, 0.56 ± 0.07 (SE) in 2009 and 0.37 ± 0.07 (SE) in 2010.

The estimated site occupancy did not differ significantly ($p=0.16$) between 2006 and 2007, whereas it differed ($p=0.009$) between 2007 and 2009, 2009 and 2010 ($p=0.03$).

DISCUSSION

Estimating populations of species that cannot be identified individually is difficult. Estimating abundance from Royle-Nichols heterogeneity models was found to be more appropriate for our study as dhole cannot be identified by any unique marking pattern. The estimated dhole density, i.e., 3.3 ± 1.2 /100 sq. km in the present study was found lower than Bandipur (Johnsingh 1983), Mudumalai (Ramesh 2010), PTR (Acharya *et al.* 2007), Mudumalai (Venkatraman *et al.* 1995) and Nagarhole (Karanth 1993) (Table 2). According to Acharya *et al.* 2007, within peninsular India, dholes are encountered specifically in dense forests and thick scrub

Table 1: Summary of dhole abundance estimates (Individuals/100 sq. km) in Pench landscape, central India

Parameters	Value
Sampling area (sq. km)	4,300
Detection probability or r	0.74 ± 0.09
Average abundance \pm SE	0.24 ± 0.08
Occupancy	0.21 ± 0.06
Average pack size \pm SE	13.9 ± 1.4
Number of individual \pm SE (/100 sq. km)	3.33 ± 1.2

*SE= Standard Error

Table 2: Estimated Dhole densities (individuals/100 sq. km) from different Protected Areas in the Indian subcontinent

Locations (Authors and year)	Study Area (sq. km)	Density/ 100 sq. km	Pack Size Range	Method
Mudumalai (Ramesh 2010)	107	43.0 ±21.0	1-28	Vehicle Transect
Mudumalai (Venkatraman <i>et al.</i> 1995)	321	31.2 ±-	4-25	Direct observation
Bandipur (Johnsingh 1982)	20	35-90	7-18	Direct observation
Nagarhole (Karanth 1993)	100	14.0 ±-	3-10	Direct observation
Pench TR (Acharya <i>et al.</i> 2007)	410	29.0 ±2.0	1-14	Radio Telemetry and direct observation
Nilgiri Plateau (Cohen <i>et al.</i> 1978)			1-5	Direct observation
Present study	4,300	3.3 ±1.2	1-29	Estimated abundance using Royle and Nichols heterogeneity model

jungles (Krishnan 1972; Davidar 1974), unlike the wild dogs of the African savannah. In most of the sites (Table 2), studies were conducted in well-managed habitat with high prey density and smaller area (20 sq. km to 410 sq. km), whereas our study area was large and covered gradient of forest and variable prey density (low to high). The earlier study on population estimation of dhole (Acharya *et al.* 2007) was restricted inside the PNP and PWS. The estimated high site occupancy (>80%) of dholes in the intensive study area (PNP and PWS) by the present study is attributed to high abundance of wild prey and well-managed habitat (Biswas and Sankar 2002, Jhala *et al.* 2010). Our findings also provided insights on conservation of large carnivores outside the PTR, as comparatively high dhole signs were encountered (>0.12/100 sq. km) inside the PTR, whereas very low sign intensity (<0.0001/100 sq. km) was encountered outside the PTR (Fig. 1).

Conservation implication

The dhole has been facing a variety of threats from humans. Encroachments by humans into its forested habitat for agriculture, stealing of kills, cattle grazing, fodder, fuelwood, and non-timber forest products collection have pushed the dhole to high degree of isolation and even local extinction (Johnsingh 1985, Acharya *et al.* 2007). More so, increasing cases of poisoning, poaching and resultant prey depletion may have contributed greatly to hasten the dholes' decline (Fox 1984), making it go the way of the African wild dog (*Lycan pictus*). Durbin *et al.* (2004) reported diseases are significant threat in South Asia, particularly those transmitted from feral

or domestic dogs, e.g., canine distemper and mange. Acharya *et al.* (2007) reported the greatest threat to dholes is from the domestic and feral dogs all around the Pench Tiger Reserve, Madhya Pradesh. Both Qureshi *et al.* (2006) and Jhala *et al.* (2010) reported that Pench landscape has forest connectivity with Kanha landscape and Satpura landscape, and forms an important conservation unit for large carnivores in central Indian landscape. The reported occupancy of dhole in overall Central Indian landscape was 85,962 sq. km in 2006 (Jhala *et al.* 2008) and 71,817 sq. km in 2010 (Jhala *et al.* 2010). Though Wildlife (Protection) Act of 1972 has helped to check the drastic decline of the dhole in many reserves within India (Ginsberg and Macdonald 1990), our study revealed that occupancy of dhole was high inside the Pench Protected Area (i.e., PNP and PWS), but low and patchy outside. As dhole population is observed fragmented, linkage between different protected areas in this landscape is crucial for long term survival of the dhole.

ACKNOWLEDGEMENTS

This study is a part of an ongoing research project 'Ecology of tiger in Pench Madhya Pradesh'. We would like to thank the Madhya Pradesh Forest Department, National Tiger Conservation Authority (NTCA), Director and Dean Wildlife Institute of India. A special thanks to all the forest officials and ground level staff of Pench Tiger Reserve, Madhya Pradesh, Forest Circle Seoni and Chhindwar. Our field assistants are also acknowledged for their support for field data collection.

REFERENCES

- ACHARYA, B.B., K. SANKAR & A.J.T. JOHNSINGH (2007): Ecology of the dhole (*Canis alpinus* Pallas) in Central India, Final Report, Wildlife Institute of India, Dehradun, 110 pp.
- ANDELT, W.F. (1985): Behavioral ecology of coyotes in South Texas *Wild. Monogr.* 94: 1-45.
- BISWAS, S. & K. SANKAR (2002): Prey abundance and food habit of tiger (*Panthera tigris tigris*) in Pench National Park, Madhya Pradesh, *India. J. of Zool (London)* 256: 411-420.
- CARBONE, C., S. CHRISTIE, K. CONFORTI, T. COULSON, N. FRANKLIN, J.R. GINSBERG, M. GRIFFITHS, J. HOLDEN, K. KAWANISHI, M. KINNAIRD, R. LAIDLAW, A. LYAM, D.W. MACDONALD, D. MARTYE, C. MCDONALD, L. NATHI, T. B'RIEN, J. SEIDENSTICKER, D.J.L. SMITH, M. SUNQUIST, R. TILSON, N. WAN & W. SHAHRUDDIN (2001): The use of photographic rates to estimate densities of tiger

- and other cryptic mammals. *Animal Conservation* 4: 75-79.
- CAUGHLEY, G. & A.R.E. SINCLAIR (1994): *Wildlife ecology and management*. Blackwell Science, Cambridge, Massachusetts, USA. 333 pp.
- CHAMPION, H.G. & S.K. SETH (1968): A revised survey of the forest types of India. Manager of Publications, Govt. of India Press, New Delhi. 404 pp.
- COHEN, J.A., M.W. FOX, A.J.T. JOHNSINGH & B.D. BARNETT (1978): Food habits of the dhole in south India. *J. of Wildlife Management* 42: 933-936.
- DAVIDAR, E.R.C. (1974): Observation at the dens of the dhole or Indian wild dog (*Cuon alpinus*). *J. Bombay Nat. Hist. Soc.* 71: 183-187.
- DUNGARIYAL, N.S. (2008): Management Plan of Pench Tiger Reserve, Madhya Pradesh. 233 pp.
- DURBIN, L.S., A. VENKATARAMAN, S. HEDGES, W. DUCKWORTH (2004): Dhole. Pp. 210-219. In: Sillero-Zubiri, C., M. Hoffmann & D.W. Macdonald (Eds): *Canids: Foxes, Wolves, Jackals and Dogs*. IUCN-SSC Canid Specialist Group, Gland, Switzerland.
- EDGAONKAR, E. (2008): Ecology of the Leopard *Panthera pardus* in Bori Wildlife Sanctuary and Satpura National Park, India. Ph.D. Thesis. University of Florida, 135 pp.
- FOX, M.W. (1984): *The Whistling Hunters: Field Studies of the Asiatic Wild dog (Cuon alpinus)*. State University of New York Press, Albany. 85 pp.
- GINSBERG, J.R. & D.W. MACDONALD (1990): Foxes, wolves, jackals and dogs: an action plan for the conservation of canids. Gland, Switzerland. IUCN. 116 pp.
- HARIHAR, A., B. PANDAV & S.P. GOYAL (2009): Density of leopards (*Panthera pardus*) in the Chilla Range of Rajaji National Park, Uttarakhand, India. *Mammalia* 73: 68-71.
- JHALA, Y.V., R. GOPAL & Q. QURESHI (2008): Status of tigers, co-predators and prey in India. National Tiger Conservation Authority, Govt. of India, New Delhi, and Wildlife Institute of India, Dehradun. TR 2011/003, 302 pp.
- JHALA, Y.V., Q. QURESHI, R. GOPAL & P.R. SINHA (2010): Status of tigers, co-predators and prey in India. National Tiger Conservation Authority, Govt. of India, New Delhi, and Wildlife Institute of India, Dehradun. TR 08/001, 151 pp.
- JHALA, Y.V., Q. QURESHI & R. GOPAL (2011): Can the abundance of tigers be assessed from their signs? *J. of Appl. Ecol.* 48: 14-24.
- JOHNSINGH, A.J.T. (1982): Reproductive and social behaviour of dhole. *J. of Zool. (Lond)* 198: 443-463.
- JOHNSINGH, A.J.T. (1983): Large mammalian prey-predator in Bandipur. *J. Bombay Nat. Hist. Soc.* 80: 1-57.
- JOHNSINGH, A.J.T. (1985): Distribution and status of dhole *Cuon alpinus* Pallas, 1811 in South Asia. *Mammalia* 49: 203-208.
- KARANTH, K.U. (1993): Predator-prey relationship among large mammals of Nagarhole National Park, Ph.D. Thesis. Mangalore University. 180 pp.
- KARANTH, K.U. (1995): Estimating tiger (*Panthera tigris*) populations from cameras trap data using capture-recapture models. *Biological Conservation* 71: 333-338.
- KELLY, M.J., A.J. NOSS, M.S. BITETTI, L. MAFFEI, R.L. ARISEPE, A. PAVIOLO, C.D. DE ANGELO & Y.E. DI BLANCO (2008): Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, and Belize. *J. of Mammalogy* 89: 408-418.
- KOHN, M.H., E.C. YORK, D.A. KAMRADT, G. HAUGHT, R.M. SAUYAOT & R.K. WAYNE (1999): Estimating population size by genotyping faeces. *Proc. R. Soc. Lond. B* 266 1420 657-663, doi:10.1098/rspb.1999.0686, pp. 1471-2954.
- KRISHNAN, M. (1972): An ecological survey of the larger mammals of peninsular India. Part II. *J. Bombay Nat. Hist. Soc.* 69: 26-54.
- MACKENZIE, D.T., J.D. NICHOLS & G.B. LACHMAN (2002): Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83: 2248-2255.
- MARNEWICK, K., P.J. FUNSTON & K.U. KARANTH (2008): Evaluating camera trapping as a method for estimating cheetah abundance in ranging areas. *S. Afri. J. of Wild Res.* 38(1): 59-65.
- MECH, L.D. (1977): Population trend and winter deer consumption in a Minnesota wolf pack. Pp. 55-83. In: Phillips, R.L. and C. Jonkel (Eds): *Proc. (1975). Predator Symposium Mont. For. Conservation Exp. Station, Univ. Montana, Missoula*. Pp. 55-83
- MITHTHAPALA, S., J. SEIDENSTICKER & S.J. O'BRIEN (1996): Phylogeographic subspecies recognition in leopards (*Panthera pardus*): Molecular genetic variation. *Conservation Biology* 10: 1115-1132.
- MONDAL, K. (2006): Leopard and ungulate abundance estimation in Rajaji National Park, Uttarakhand. Masters Thesis. Forest Research Institute (Deemed University) Dehradun. 95 pp.
- NOWELL, K. & P. JACKSON (1996): *Wild Cats: status survey and Conservation Plan*. IUCN, Gland, Switzerland. 382 pp.
- RAMESH, T. (2010): Prey Selection and Food habits of large carnivores (Tiger, Leopard and Dhole) in Mudumalai Tiger Reserve, Western Ghat, India. Ph.D. Thesis, Saurashtra University, 178 pp.
- RODGERS, W.A. & H.S. PANWAR (1988): Planning wildlife protected area network in India, Vol II, State summaries. A report prepared for the Department of Environment, Forests and Wildlife, Government of India and Wildlife Institute of India. Pp. 217-230.
- ROYLE, J.A. & J.D. NICHOLS (2003): Estimating abundance from repeated presence absence data or point counts. *Ecology* 84: 777-790.
- ROWCLIFFE, J.M., J. FIELD, S.T. TURVEY & C. CARBONE (2008): Estimating animal density using camera traps without the need for individual recognition. *J. App. Ecol.* 45: 1228-1236.
- SANKAR, K., Q. QURESHI, M.K.S. PASHA & G. ARENDRAN (2001): Ecology of gaur (*Bos gaurus*) in Pench Tiger Reserve, Madhya Pradesh. Final report. Wildlife Institute of India, Dehradun. 124 pp.
- SHARMA, R.K., Y.V. JHALA, Q. QURESHI, J. VATTAKAVEN, R. GOPAL & K. NAYAK (2010): Evaluating capture-recapture population and density estimation of tigers in a population with known parameters. *Animal Conservation* 13: 94-103.
- SOISALO, M.K. & S.M.C. CAVALCANTI (2006): Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture-recapture sampling in combination with GPS radio-telemetry. *Biological Conservation* 129: 487-496.
- QURESHI, Q., R. GOPAL, S. KYATHAM, S. BASU, A. MITRA & Y.V. JHALA (2006): Evaluating Tiger Habitat at the tehsil level. Project Tiger Directorate, Govt. of India, New Delhi, and Wildlife Institute of India, Dehradun, TR No.06/001, 162 pp.
- VENKATARAMAN, B.A., R. ARUMUGAM & R. SUKUMAR (1995): The foraging ecology of dhole (*Cuon alpinus*) in Mudumalai Sanctuary, southern India. *J. of Zool.* 237: 543-561.
- WIKRAMNAYEKE, E.D., E. DINERSTEIN, J.G. ROBINSON, U. KARANTH, A.R. RABINOWITZ, D. OLSON, T. MATHEW, P. HEDAO, M. CONOR, G. HEMELEY & D. BLOZE (1998): An ecology based approach to setting priorities for conservation of tigers *Panthera tigris*, in the wild. *Conservation Biology* 12: 865-878.
- ZAR, J.H. (1984): *Biostatistical analysis*. 2nd edn. Englewood Cliffs, NJ: Prentice Hall, 130 pp.

